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PROTOGASTER, REPRESENTING A NEW ORDER OF THE GASTEROMYCETES¹

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A most interesting Gasteromycete was discovered by the late Dr. Roland Thaxter at Kittery Point, Maine, August, 1895. Dr. Thaxter applied to this fungus the generic name, *Protogaster*. Its tiny subspherical fructifications were found from one to three inches below the surface of the ground, attached to or "running from the roots of the cultivated pansy." In a letter to the writer under date of March 15, 1932, Dr. Thaxter said "The fungus seems a very curious and interesting one. It appeared to be definitely a parasite on the roots of *Viola*." It is, indeed, an interesting Basidiomycete!

In one collection (5661) Dr. Thaxter had preserved intact a clod of soil glued to the bottom of a small pill box. Nestled in some of the crevices and hollows of the clod are groups of the basidiocarps of this fungus (pl. 7). Under the low-power binocular microscope these fructifications have the appearance of tiny cocoons of some insect or the egg-sacs of tiny spiders. They adhere to the soil or to roots by minute cobwebby hyphae which radiate in every direction from the sporophore. These

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are so numerous from the surface of very young fructifications that the surface of the latter is nearly obscured. In the more mature stages this indefiniteness becomes a more definite meshy surface. In pl. 7 such a group of sporophores in several stages of maturity is shown in close proximity to a small rootlet.

The three collections taken by Dr. Thaxter formed the basis of the studies here reported. The collections together total hundreds of the fructifications dried with some of the soil in which they were found. These gasteromycetous fruiting bodies are from 0.1 to 0.5 millimeter in diameter. The youngest ones are white, while the more mature individuals are pale brownish-drab, the surface being of a soft dry byssoid to innately fibrillose character. The loose hyphae of the surface of two or more fruiting bodies often intertwine, causing them to adhere to each other. When several are involved a bead-like series may result. This adherence, however, in all the observations made by the writer involves only the superficial hyphae of the peridium, and the internal structure remains entirely separate. Each of the bodies in these cases remains a morphologically distinct entity.

In order to study the morphology in detail several fructifications were prepared and microtome sections were made. They were put through the formal-acetic-alcohol fixative and stained with safranin-gentian violet. When saturated by a clear solution, such as formal-acetic-alcohol, the sporophores with immature spores changed merely to a creamy white, while the more mature ones having the glebal locule stuffed with spores changed immediately to a color very close to vinaceous-fawn.

The prepared slides and crushed mounts show the peridium to be a simple layer of meshy or loosely interwoven hyaline hyphae (prosenchyma) which are white to cream-colored (*sub lente*) and usually are considerably branched. The layer is 17–46 μ thick. This comprises the whole of the sterile tissue of the fruiting body except the subhymenial layer which is composed of compacted hyphae taking a deeper stain than the peridium or hymenium. This subhymenial layer is very thin, usually the thickness of two or three hyphae (2–4 μ thick).

The gleba is extremely simple, consisting of one spherical locule, the wall of which is a definite smooth hymenium composed of clavate to fusiform basidia interspersed among short-clavate paraphyses. The basidia are mostly 1-4-spored, 2-spored basidia predominating in young fruiting bodies. The basidia are $8.5-11 \times 3-7 \mu$. In cases of large accumulations of spores at maturity the gleba in general appearance assumes a clay color or Mikado brown to snuff-brown. Where compact accumulations of spores are found the spore mass assumes a color darker than indicated above.

When considered in terms of the capacity of the locule, spores are produced in large quantities. At maturity the cavity is completely filled, and there is some indication that the pressure of the spores may burst the peridium, liberating the former. As a rule the peridium doubtless disintegrates in the soil, with spore dispersal by water and possibly by insects.

The spores are most commonly pip-shaped to obovoid, but are sometimes ellipsoid with broadly rounded ends. Under the microscope they are hyaline to dilute citrinous but in mass they are from clay color to Mikado brown or snuff-brown. The exospore is rather thick and distinct. The spores measure $8-12.5 \times 3.5-6 \mu$.

This is doubtless the most simple gasteromycetous form yet discovered. The tiny subspherical sporocarps with subterranean origin and life cycle are very similar in fundamental tissues and ecological conditions (hypogeous) of development to those of the button stages (primordia) of the sporophores of more highly differentiated Gasteromycetes and angiocarpous Agaricales. The primordia of the sporocarps of the plurilocular Gasteromycetes and of the Agaricales for the most part have a hypogeous origin but further developmental stages, except for most of the Hymenogastreales, emerge to an epigeous stage at maturity. With such a recapitulation of this button-like hypogeous form in the primordial sporocarps of most of these higher fleshy fungi it would not be difficult to postulate the emergence of the epigeous forms among them from such simpler hypogeous forms as *Protogaster*.

The peridium of *Protogaster* represents all of the sterile tissue of the normal sporophore. It is a simple layer of undifferentiated prosenchyma of a rather loose mesh, the remains undoubtedly of the fundament of the developing fructification. This type of peridial structure perhaps should be interpreted as the most primitive "universal veil" or volvate tissue of the Gasteromycetes, and it can perhaps with equal truth be said to be the forerunner of the volva (blematogen) in the primordium of the angiocarpous development of certain of the Agaricaceae.

The mycelioid hyphae which radiate into the soil from the sporophore usually are not organized to any degree into rhizomorphic cords. Two, three, or four hyphae may twine loosely together to form a meshy strand, but they seem never to assume such a definite relation and close contact with each other as are maintained in an organized rhizomorph. Most, if not all, of the previously known Gasteromycetes have well-developed fibrils or rhizomorphs at the termination of certain of which the fructifications are borne.

A study of the dry herbarium material of the fungus under consideration gives little clue as to its orientation *in situ*. For the most part the fructifications are spherical or oblong, and there is *usually* no definite place of attachment discernible. In a very small percentage of basidiocarps studied there is a condition, however, which must not be overlooked in this connection. Out of twenty-seven fructifications which were studied critically, three showed the formation of a peg-like growth from the peridium into the locule. In each of these cases there was found a very inconspicuous place of attachment just below this exceptional peg-like growth. Sixty-eight additional specimens were examined *in toto* by transmitted light, by which two more were found with the growth. The peg-like growth is of the same loose structure as that of the peridium. It is not an invagination of the peridium but should doubtless be more properly interpreted as a mere tendency toward further sterile tissue. It is perhaps in fact a tendency toward a very rudimentary sterile base or even the rudiment of a columella. The one of these of which the writer has pre-

pared microtome sections extends into the locule $67\ \mu$ and is $42\ \mu$ in diameter at the base. This particular fructification is $374\ \mu$ in diameter and the locule measures $292\ \mu$ in diameter. This rudimentary columella (?) or sterile base (?) is not a constant morphological character of *Protogaster* and thus it has not been incorporated in the formal description below.

All previously described Gasteromycetes are plurilocular and therefore involve many more sterile elements, such as plates and septa in the gleba, than found in *Protogaster*. Since *Protogaster* is so unique in its morphological simplicity and unilocular character of the gleba, a new order and family are proposed to include this genus. The new order is proposed to comprise all unilocular Gasteromycetes having no specialized sterile tissues, and the family to include all of those of the new order which show no invagination, have a definite even hymenium.

Dr. Thaxter gave the genus name, *Protogaster* (*in Herb.*), and in his search for a suitable specific name he had used three, to-wit, *P. rhizophilus*, *P. radicolus*, and *P. Violae*. The writer has adopted the specific name which appears (*in Herb.*) on the collection having the lowest accession number. The diagnostic description follows:

PROTOGASTRALES Zeller, ord. nov.

Fructificationes subsphaericae, sine speciale sterile textu; peridium indehiscens; gleba uniloculata.

Fructifications spherical to subspherical, with no specialized sterile tissues present; *peridium* simple, closed; *gleba* unilocular.

PROTOGASTRACEAE Zeller, fam. nov.

Fructificationes subsphaericae, minutae; *peridium* simplex contextum, indehiscens; *gleba* uniloculata, sine invaginatione; hymenium laeve.

Fructifications small, subspherical; *peridium* of simple fundamental tissue, indehiscent; *gleba* unilocular, showing no invagination; *hymenium* smooth.

PROTOGASTER Thaxter, gen. nov.²

Fructificationes minutae, sphaericae vel subsphaericae, sine speciale sterile textu, hypogaeae; peridium simplex primordiale contextum, indehiscens; gleba uniloculata, sine invaginatione; hymenium laeve; sporae ellipsoideae vel subellipsoideae, laeves, hyalinae vel subcoloratae.

Fructifications small, spherical to subspherical, with no specialized sterile tissues, hypogeous; *peridium* of simple fundamental tissue, indehiscens; *gleba* unilocular, showing no invagination; *hymenium* smooth; *spores* ellipsoid to subellipsoid, smooth, hyaline to slightly colored.

Protogaster rhizophilus Thaxter, sp. nov.

Fructificationes sphaericae vel ellipsoideae, 100–500 μ diametro, hypogaeae, superficie arida, alba vel pallide brunneo-grisea, byssoidea vel innato-fibrillosa (sericea), unde hypoidei funiculi in soli evanescunt; peridium 17–46 μ crassitudine, simplex, byssoideum, ex hyphis tenuibus laxis undulatis; gleba uniloculata, “clay color,” “Mikado brown,” vel “snuff-brown”;³ locellus subglobosus, primo vacuus, maturitate sporis repletus; hymenium laeve; basidia inconspicua, hyalina, clavata vel fusoida, mono- vel tetraspora, vulgo dispora, 8.5–11 x 3–7 μ , sterigmatibus brevibus; sporae subellipsoideae vel obovoideae, laeves, hyalinae vel dilute citrinae *sub lente, in massa* “Mikado brown” vel “snuff-brown,” exosporo subconspicuo, 8–12.5 x 3.5–6 μ .

In terra inter radices vivas *Violae*, Kittery Point, Maine, Amer. bor. (*Roland Thaxter*). Aestate.

Type: Kittery Point, Maine, August, 1895, *Roland Thaxter* (in Thaxter Bequest (No. 5660) to Farlow Herb., Harvard University).

Fructifications spherical to ellipsoid, 100–500 μ in diameter, hypogeous, held in soil cavities by cobwebby hyphae radiating in all directions from the peridium; *surface* white to pale brownish drab, dry, byssoid to innately-fibrillose (silky); *peridium* simple, of loosely interwoven hyphae mostly parallel with the surface, hyaline, 17–46 μ thick; *gleba* unilocular, from clay color to Mikado brown or snuff-brown due to accumulation of spores; *cavity* subglobose, empty at first but stuffed with spores at maturity; *hymenium* smooth; *basidia* inconspicuous,

² The writer assumes the whole responsibility for the description of the genus and species. Dr. Thaxter left no manuscript with the herbarium material and had published nothing pertaining to *Protogaster*.

³ Ridgway's ‘Color Standard and Nomenclature’ was used throughout this paper.

hyaline, granular, clavate to fusiform, 1–4-spored (2-spored predominate in very young fruiting bodies), 8.5–11 x 3–7 μ ; spores pip-shaped, obovoid, or subellipsoid with broadly rounded ends, smooth, hyaline to dilute citrine (*sub lente*), Mikado brown to snuff-brown *en mass*, exospore rather prominent, 8–12.5 x 3.5–6 μ .

One to three inches below the surface of the soil surrounding living roots of the cultivated pansy (*Viola*), Kittery Point, Maine (*Roland Thaxter*). August.

Specimens examined:

MAINE: York County, Kittery Point, August, 1895, *Roland Thaxter*, 3282, 5660 (type), 5661 (in Thaxter Bequest to Farlow Herb., Harvard University).

Since the class, Gasteromycetes, is generally recognized as a grouping of several apparent series or lines of parallel or perhaps divergent tendencies in development, it cannot be considered as a natural single division of the fungi. For this reason it cannot be said that *Protogaster* is more primitive because of its greater simplicity than all forms exhibiting the several series of developmental tendencies in the previously described Gasteromycetes. Rather, it seems to take its place in one of the lines, namely, that with smooth ellipsoidal spores and with also a definite smooth hymenium. It seems to the writer that the most natural connection is from *Protogaster* through species of *Rhizopogon*, with their hypogeous nature, and finally through the Lycoperdales.

Connecting links may yet be discovered between *Protogaster* and *Rhizopogon*. And, too, other new forms may in time more definitely indicate the possible point or points of divergence of more primitive lines of development branching off from this main (?) trunk below *Protogaster*.

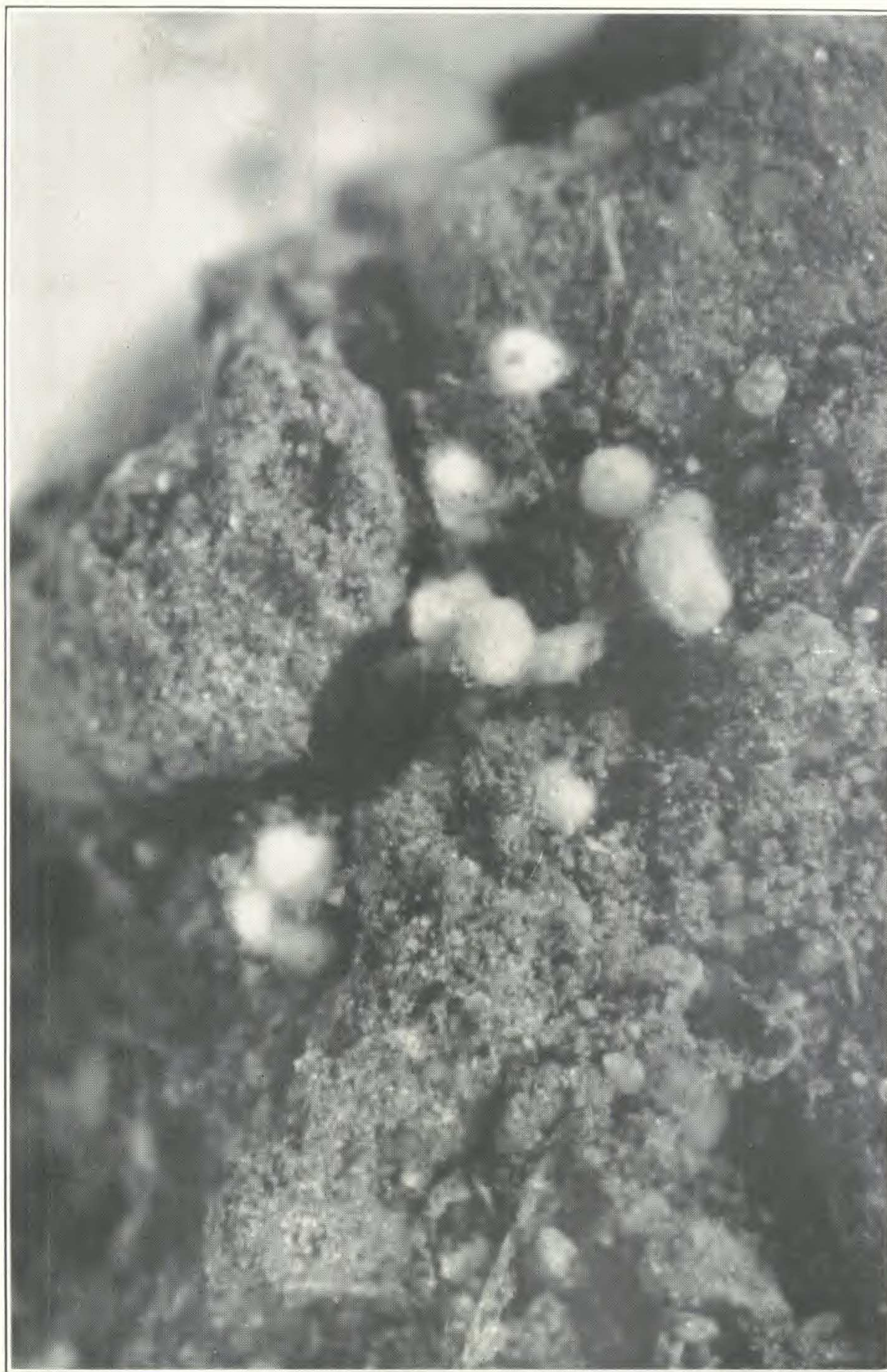
The writer is gratefully indebted to the late Dr. Roland Thaxter for the privilege of studying this most interesting fungus and to Professors J. H. Faull, W. H. Weston, Jr., and Oakes Ames, committee administering the Farlow Herbarium, for their cooperation in putting the herbarium material at his disposal.

EXPLANATION OF PLATE

PLATE 7

Protogaster rhizophilus Thaxter

Sporophores in a crevice and hollow on the surface of a clod of soil taken 2 to 3 inches below ground, Kittery Point, Maine, August, 1895. (*Roland Thaxter*). About $\times 32$. Photograph by Dr. Frank P. McWhorter.



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EXPLANATION OF PLATE

PLATE 8

Protogaster rhizophilus Thaxter

Fig. 1. Diagrammatic median section of a basidiocarp, illustrating the relation of morphological parts. \times about 300.

Fig. 2. Diagrammatic sketch of the peg-like growth of fundamental tissue rarely found to extend into the locule. \times about 300.

Fig. 3. Drawing to scale of a section through the peridium and subhymenial layer, showing the relation to basidia and paraphyses, highly magnified. \times about 3000.